Seasonal Flight Pattern of the Western Balsam Bark Beetle, Dryocoetes confusus Swaine (Coleoptera: Curculionidae), in Central British Columbia

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ABSTRACT

Seasonal flight pattern of the western balsam bark beetle, *Dryocoetes confusus* Swaine, in stands of subalpine fir, *Abies lasiocarpa* (Hook) Nutt., in north–central British Columbia was monitored for three years using multiple-funnel traps baited with (±)-*exo*-brevicomin. Two major flight periods occurred per year, the first commencing in mid- to late June, and the second occurring in mid- to late August. The first flight was predominantly males, while the second flight was composed primarily of females, probably re-emerged parent adults. Little flight occurred until within-stand temperatures exceeded 15°C. Traps placed 6 m above the ground caught four times as many beetles as traps placed 2 m above the ground. Our results indicate that semiochemical-based manipulation of the western balsam bark beetle should be implemented by early May.

Key Words: Coleoptera: Curculionidae, Scolytinae

INTRODUCTION

The western balsam bark beetle, Dryocoetes confusus Swaine, occurs throughout the range of its host, subalpine fir, Abies lasiocarpa (Hook) Nutt., from British Columbia to New Mexico (Bright 1963). The beetle is the most destructive insect pest of mature and overmature subalpine fir in British Columbia (Garbutt 1992).

Mathers (1931) described a two-year life cycle for D. confusus in central B.C. First emergence of new adults occurs in late June, and continues throughout July. These adults attack fresh host material, with the attacking males excavating nuptial chambers. Male D. confusus are polygamous, and mate with up to four females (Bright 1976). Females excavate brood tunnels and lay eggs until "well into August" (Mathers 1931). After egg laying is completed, the parent adults extend brood tunnels by feeding, creating tunnels in which they overwinter. The following spring, females lay a second brood in a continuation of these same tunnels. Parent adults then reemerge in mid-July to attack fresh material,

and lay a third brood. Eggs of the first brood hatch in late August, overwinter as small larvae, develop to teneral adults, and overwinter again. Progeny of the second brood, beginning early the second summer, develop in a similar way. The third brood, beginning late in the second summer, begins to hatch by the third week in August (Mathers 1931). Thus, Mathers (1931) identified two clearly defined flight periods, of which the second had re-emerging adults.

Baited multiple-funnel traps have been used to monitor *D. confusus* flight periods for three years in Utah, USA (Hansen 1996), and for three years in northern Idaho and western Montana, USA (Gibson *et al.* 1997). Both studies identified two flight peaks, with the main part of the first peak occurring from mid-June to early July, and the second variably in August to September. In Utah, the relative size of the two flight peaks varied across elevations, with a trend towards larger first peaks at higher elevations, and larger second peaks at lower elevations. Both studies

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noted a larger percentage of male beetles in the early-season flight, and a trend towards more females in the later season flight.

Hansen (1996) noted that very little flight occurred when ambient temperatures were less than 15°C, although low temperatures were

not a factor separating the two seasonal flight peaks.

Our objectives were to describe the seasonal flight patterns of *D. confusus* and to assess the vertical distribution of within-stand flight in central British Columbia.

MATERIALS AND METHODS

Eight-unit multiple-funnel traps (Lindgren 1983) were set in the Bulkley Valley, central British Columbia, in the Engelmann Spruce-Subalpine Fir or Sub-Boreal Spruce biogeoclimatic zones (Banner et al. 1993), annually in 1985, 1986, and 1987. Trapping periods and locations for monitoring seasonal flight were 19 June–22 August 1985 (10 traps) at McKendrick Pass, 13 June-27 August 1986 (6 traps), at Gramophone Creek, and 28 May-27 August 1987 (10 traps) at Kwun Creek. Traps were suspended on ropes between two trees in stands with active beetle infestations. and were placed at least 50 m apart. The top of each trap was hung approximately 2 m above ground in 1985 and 1986. Based on results from 1986 of vertical distribution of withinstand flights, the top of each trap was raised to 3 m in 1987. Attractive baits used in each trap were the aggregation pheromone (±)-exobrevicomin (Albany International, Columbus, Ohio) 99.7% purity (Borden et al. 1987), in two glass capillary tubes, collectively releasing 0.4 mg/24 h in 1985 and 1986. Based on results from experiments in 1986

(Stock *et al.* 1995), the release rate of trap baits was increased to four capillary tubes, collectively releasing 0.8 mg/24 h ((±)-*exo*-brevicomin, 98.0% purity, Contech Inc., Delta, B.C.) in 1987. Captured *D. confusus* were counted and sexed daily in 1985, and on Mondays, Wednesdays, and Fridays in 1986 and 1987. Within-stand temperature and relative humidity patterns were monitored with a hygrothermograph (C.F. Casella and Co., London, UK, Model 3083/TT) placed in a Stevens box located under the canopy on the ground near the funnel traps.

In a separate experiment in 1986, 10 exobrevicomin-baited 8-unit multiple-funnel traps spaced 50 m apart were set out at Gramophone Creek. Five traps were selected randomly to be suspended approximately 2 m above ground, and five to be suspended approximately 6 m above ground. The experiment was established on 19 June, and ended on 11 July.

Data from the trap height experiment were compared using a t-test (Number Cruncher Statistical System 1988).

RESULTS

Seasonal flight patterns (Fig. 1) indicated that D. confusus has at least two flight periods each summer. The first (main) flight period occurred in mid- to late June, and the second in mid-August. Flight had probably started prior to trap placement in 1985 and 1986, as evidenced by catches in the first collection period. Peaks in flight activity generally occurred when maximum daily ambient temperature was 15°C or warmer (Fig. 1). Relatively little flight occurred in the interval between flight peaks, despite apparently adequate maximum temperatures. The trends for cumulative captures were roughly similar each year, showing a slow rise followed by a sharp increase, with the pattern then repeating itself (Fig. 2). By assuming a separation of the two flights on 1 August, the second flight represented 19% of total flight in 1985, 17% of total flight in 1986, and 26% of total flight in 1987. Small numbers of beetles flew in September in all years after the traps had been taken down (pers. observations).

Cumulatively, for the three years of study, less than 5% of total trap catch occurred when daily maximum temperatures within stands were less than 15°C.

The overall proportion of captured males was 0.46 in 1985, 0.67 in 1986, and 0.44 in 1987 (Fig. 3). However, males predominated early in the season, and the sex ratio became progressively female-biased over time. The

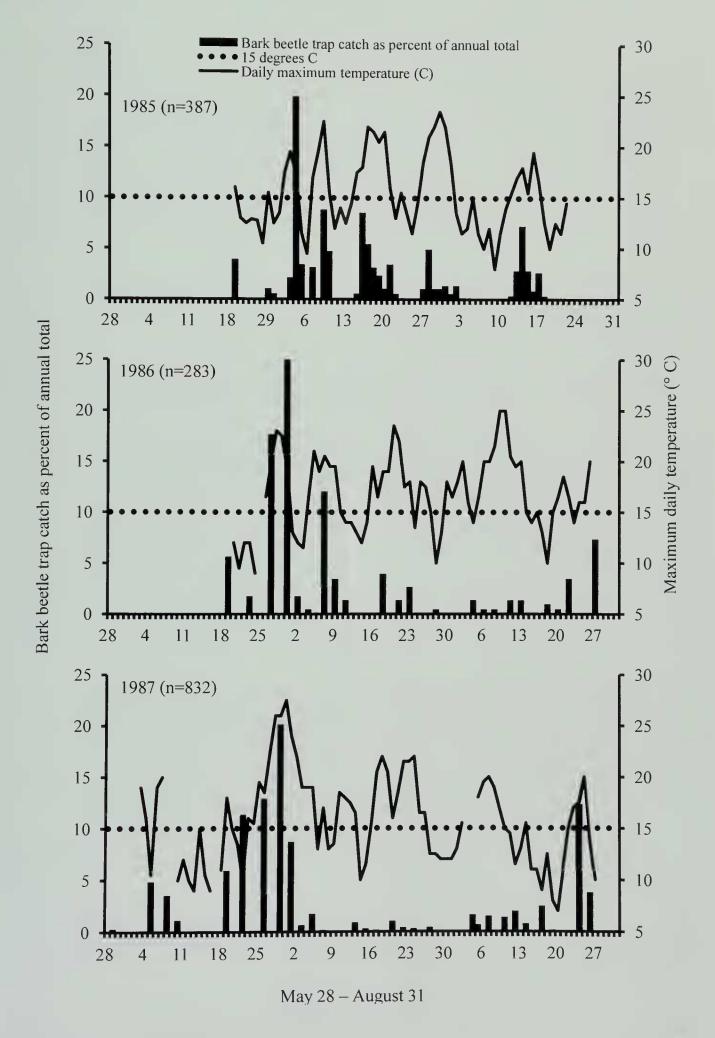


Figure 1. Seasonal flight patterns and maximum daily temperatures for *Dryocoetes confusus* caught in *exo*-brevicomin–baited multiple funnel traps at Gramophone Creek, B.C., 1985–1986, and Kwun Creek, B.C., 1987.

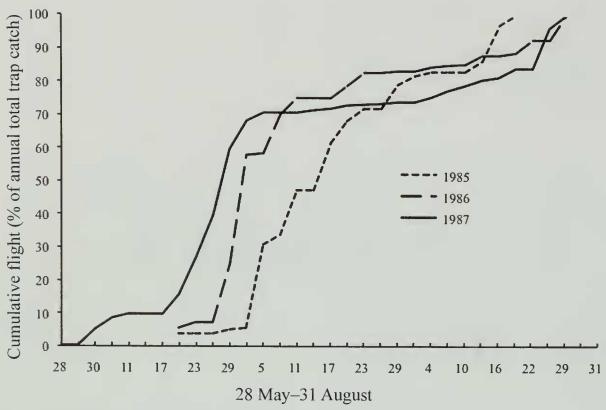


Figure 2. Cumulative trap catch as percent of annual total trap catch for *Dryocoetes confusus* caught in *exo*-brevicomin–baited multiple funnel traps at Gramophone Creek, B.C., 1985–1986, and Kwun Creek, B.C., 1987.

less well-defined trend in 1986 could be due to the generally cooler weather early in the summer, which may have affected the emergence of one of the sexes. Also, there were relatively few beetles caught in 1986 (Fig. 1), which may have increased variation, resulting in weaker trends (see also Fig. 2).

Approximately four times more beetles were captured in traps at the 6 m height than at 2 m (Table 1).

DISCUSSION

The evidence that the main flight period of the western balsam bark beetle occurs primarily in mid- to late June corresponds well with Mathers' (1931) data on life history. Some caution may be needed when interpreting results of pheromone-baited funnel traps for monitoring scolytid flight periods (Bentz 2006). Pheromone-baited traps within stands may catch disproportionately more beetles during periods of reduced beetle flight, and disproportionately fewer beetles during peak beetle flight, producing an "elongated" flight period that may not coincide well with actual beetle emergence from trees (Bentz 2006). However, for semiochemical-based management, it is necessary to know when beetle flight actually commences in stands, and we are confident our results indicate that D. confusus flight can begin in early June or late May (Fig. 1), when ambient temperatures are higher than 15°C.

This temperature threshold is consistent with Hansen (1996) and Negrón and Popp (2009). Hansen (1996) noted that snow was mostly gone before flight commenced. The occurrence of the second peak in mid-August in central BC, however, was one month later than the mid-July re-emergence described by Mathers (1931). This may have been due to weather. Temperature-driven variation in development is common in other scolytid species: it can shorten their life cycles when warm weather permits, or lengthen them to endure periods of cold (Amman 1973; Schmid and Frye 1977; Langor 1987; Wermelinger and Seifert 1999). Flight peaks of the western balsam bark beetle appear to be variable across the landscape and highly weather dependent (Hansen 1996; Gibson et al. 1997; Negrón and Popp 2009). This information should prompt further investigations to discover if D. confusus can indeed develop on

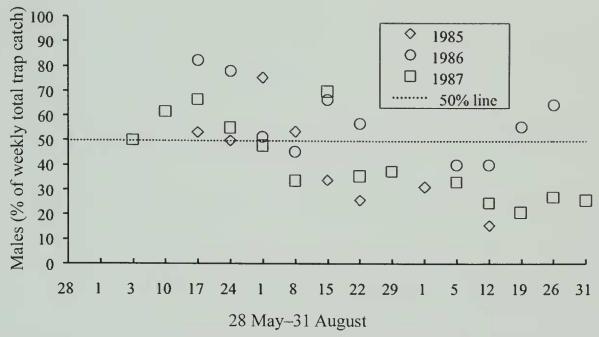


Figure 3. Seasonal variation in the male component of flying *Dryocoetes confusus* populations, Gramophone Creek, B.C., 1985–1986, and Kwun Creek, B.C., 1987.

a one-year cycle, as suggested by Bright (1963), and which does occur in *Dryocoetes autographus* (Johansson *et al.* 1994) and the spruce beetle, *Dendroctonus rufipennis* (Schmid and Frye 1977). Such a life cycle may become more prevalent under conditions of global warming. Further work is also necessary to assess efficacy of baited funnel traps for monitoring beetle flight, as per Bentz (2006). It is essential to understand variability in life-cycle duration and flight periods in order to implement pest management tactics, e.g., semiochemical-based population manipulation, effectively.

The period between flight peaks corresponds to when females in galleries are laying a second brood (Mathers 1931) and/or feeding to regenerate their flight muscles (Chapman 1957; Borden and Slater 1969; Bhakthan *et al.* 1970; Bhakthan *et al.* 1971). Exact information on when first-, second-, or third- brood beetles are represented in flying populations at higher latitudes awaits further study.

The overall proportions of captured males conformed well to the 0.43 proportion of males in emerging beetle broods (Stock 1981). There was no evidence for an early emergence of the responding sex (females; Fig. 3), considered to be an outbreeding mechanism in other scolytids (Cameron and Borden 1967; Billings and Gara 1975; Borden 1982). Rather, there is evidence for early emergence of the pioneering sex (males; Fig. 3), which is

consistent with Hansen (1996) and Negrón and Popp (2009). Early emergence of the pioneering sex has been shown for summer brood *Ips typographus* L. (Botterweg 1983) and *I. perturbatus* (Graves 2008). It is possible that in uneven-aged multi-storied old-growth subalpine forests, the patchy and temporary nature of the host resource (newly susceptible or freshly downed trees; Bleiker et al. 2003, 2005) may force beetle populations to search over large areas. Early emerging males could establish new attraction centres, resulting in multiple matings with local females and enhanced population genetic heterogeneity (Flamm et al. 1987). If the responding sex were to emerge first in such a harsh environment, the uncertainty of initial attack success, establishment of secondary attraction, and ultimately mass-aggregation (Borden et al. 1986) could be increased, resulting in high mortality of the responding sex during dispersal. Subsequent re-emergence of females late in the summer may further enhance genetic heterogeneity (Cameron and Borden 1967).

We hypothesize that a significant proportion of the second flight is comprised of re-emerging adults. Flamm *et al.* (1987) found that 75% and 64% of attacking *Ips avulsus* Eichoff and *I. calligraphus* Germar, respectively, re-emerged from original host trees, and that males represented only 27.8% of re-emerging *I. avulsus*, compared to 46.7% of re-emerging *I. calligraphus*. Anderbrandt *et*

Table 1
Catch of *D. confusus* in a five-replicate experiment with 8-unit (±)-*exo*-brevicomin–baited funnel traps set at 2 and 6 m above ground, 19 June–11 July 1986, Gramophone Creek, B.C.

	Total number of beetles per trap (Mean \pm S.E.)a	
Trap height	Males	Females
2m	$15 \pm 3.0a$	5 ± 1.8a
6m	$49 \pm 9.8b$	$29 \pm 7.2b$

a Means within columns followed by the same number are not significantly different, t-test, $p \le 0.0250$.

al. (1985) found that about 84% of *I. typographus* reemerged, of which about 36% were males. It is possible that those females fit enough to re-emerge gain an adaptive advantage by exploiting unused bark in previously attacked, but not fully utilized trees (Flamm *et al.* 1987). A portion of the second flight peak may also be generated by broods originating in downed materials (Negrón and Popp 2009), if development were delayed because of snow cover.

Our results indicate that pest management tactics such as semiochemical-based management (Stock et al. 1990, 1993, and 1995; Maclauchlan et al. 2003; Jeans-Williams and Borden 2006) need to be implemented by early May. Finer-scale silvicultural approaches such as group selection or small patch harvesting (Veblen et al. 1991; Stock et al. 1993; Maclauchlan et al. 2003) would need to account for the period when re-emerged, and presumably gravid, females are active; e.g., delay implementation until September.

The tendency of *D. confusus* to fly well above ground within stands has been shown

for other scolytid species. Beetles with such flight patterns presumably avoid the impediments of understorey vegetation and dense tree crowns, and are positioned to intercept pheromone plumes (Ashraf and Berryman 1969; Schmitz et al. 1980; Amman and Cole 1983; Bartos and Amman 1989). Understorey vegetation can be 3 or 4 m high in subalpine forests. Waters and Stock (1995) counted attack densities at 1.3, 4 and 8 m height, and found that beetle attacks per square metre were greatest at 4 m above ground, although the difference between heights was not significant. Flight height may not be correlated to attack success, although Maclauchlan et al. (2003) hypothesize that cool nighttime temperatures near the ground or wetness and non-vectored fungal development under the bark may limit gallery success in the lower two metres of the bole.

It would be useful to know, for semiochemical-based manipulation of *D. confusus* populations, what relationship this flight pattern might have to the initial attack height and vertical distribution of attack density by *D. confusus* on standing trees.

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REFERENCES

Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. Environmental Entomology 2:541–547.

Amman, G. D., and W. E. Cole. 1983. Mountain pine beetle dynamics in lodgepole pine forests Part II: Population

- dynamics. USDA Forest Service Intermountain Forest and Range Experiment Station, Ogden, Utah. General Technical Report INT-145. 59 p.
- Anderbrandt, O., F. Schlyter, and G. Birgersson. 1985. Intraspecific competition affecting parents and offspring in the bark beetle *Ips typographus*. Oikos 45:89–98.
- **Ashraf, M., and A. A. Berryman. 1969.** Biology of *Scolytus ventralis* (Coleoptera: Scolytidae) attacking *Abies grandis* in northern Idaho. Melanderia 2:1–23.
- Banner, A., W. MacKenzie, S. Haeussler, S. Thomson, J. Pojar, and R. Trowbridge. 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. B.C. Ministry of Forests, Research Branch, Victoria, B.C., Land Management Handbook No. 26. 152 pages.
- Bartos, D. L., and G. D. Amman. 1989. Microclimate: an alternative to tree vigor as a basis for mountain pine beetle infestations. USDA Forest Service Res. Pap. Int-400. Ogden, Utah. 10 p.
- **Bentz**, **B. J. 2006.** Mountain pine beetle population sampling: inferences from Lindgren pheromone traps and tree emergence cages. Canadian Journal of Forest Research 36:351–360.
- Bhakthan, N. M. G., J. H. Borden, and K. K. Nair. 1970. Fine structure of degenerating and regenerating flight muscles in a bark beetle, *Ips confusus*. I. Degeneration. Journal of Cell Sciences 6:807–819.
- Bhakthan, N. M. G., K. K. Nair, and J. H. Borden. 1971. Fine structure of degenerating and regenerating flight muscles in a bark beetle, *Ips confusus*. II. Regeneration. Canadian Journal of Zoology 49:85–89.
- Billings, R. F., and R. I. Gara. 1975. Rhythmic emergence of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) from two host species. Annals of the Entomological Society of America 68:1033–1036.
- Bleiker, K. P., B. S. Lindgren, and L. E. Maclauchlan. 2003. Characteristics of subalpine fir susceptible to attack by western balsam bark beetle (Coleoptera: Scolytidae). Canadian Journal of Forest Research 33(8):1538–1543.
- Bleiker, K. P., B. S. Lindgren, and L. E. Maclauchlan. 2005. Resistance of fast- and slow-growing subalpine fir to pheromone-induced attack by western balsam bark beetle (Coleoptera: Scolytinae). Agricultural and Forest Entomology 7(3):237–244.
- **Borden, J. H. 1982.** Aggregation pheromones, pp. 74–139. *In* J. B. Mitton and K. B. Sturgeon (Eds.). Bark beetles in North American conifers: A system for the study of evolutionary biology. University of Texas Press, Austin, TX. 527 p.
- Borden, J. H., and C. E. Slater. 1969. Flight muscle volume change in *Ips confusus* (Coleoptera: Scolytidae). Canadian Journal of Zoology 47:29–32.
- Borden, J. H., D. W. A. Hunt, D. R. Miller, K. N. Slessor. 1986. Orientation in forest Coleoptera: an uncertain outcome of responses by individual beetles to variable stimuli, pp. 97–109. *In* T. L. Payne, M. C. Birch, and C. E. J. Kennedy (eds.). Mechanisms in insect olfaction. Clarendon Press, Oxford.
- Borden, J. H., A. M. Pierce, H. D. Pierce, Jr., L. J. Chong, A. J. Stock, and A. C. Oehlschlager. 1987. Semiochemicals produced by the western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). Journal of Chemical Ecology 13:823–836.
- **Botterweg, P. F. 1983.** The effect of attack density on size, fat content, and emergence of the spruce bark beetle *Ips typographus* L. Z. ang. Entomology 96:47–55.
- **Bright, D. R., Jr. 1963.** Bark beetles of the genus *Dryocoetes* (Coleoptera: Scolytidae) in North America. Annals of the Entomological Society of America 56:103–115.
- **Bright**, **D.R.**, **Jr. 1976**. The insects and arachnids of Canada and Alaska. 2. Coleoptera: Scolytidae. Canadian Department of Agriculture Publication No. 1576. 241 p.
- Cameron, E. A., and J. H. Borden. 1967. Emergence patterns of *Ips confusus* (Coleoptera: Scolytidae) from ponderosa pine. The Canadian Entomologist 99:236–244.
- **Chapman, J. A. 1957.** Flight muscle change during adult life in the Scolytidae. Canadian Department of Forestry, Division of Forest Biology. Bi-monthly Progress Report 13:3–4.
- Flamm, R. O., S. P. Cook, T. L. Wagner, P. E. Pulley, and R. N. Coulson. 1987. Reemergence and emergence of *Ips avulsus* and *Ips calligraphus* (Coleoptera: Scolytidae). Environmental Entomologist 16:869–876.
- Garbutt, R. 1992. Western balsam bark beetle. Forest Pest Leaflet 64. Canadian Forest Service, Pacific Forestry Centre, Victoria, BC. 4 p.
- Gibson, K., S. Kegley, and B. Oakes. 1997. Western balsam bark beetle activity and flight periodicity in the Northern Region. USDA Forest Service Cooperative Forestry and Forest Health Protection, Missoula, MT. Report 97-3. 5 p.
- Graves, A. D. 2008. The chemical ecology of the northern spruce engraver, *Ips perturbatus* (Eichoff) (Coleoptera: Scolytidae), and associated insects in spruce forests of Alaska. Doctoral Dissertation, University of Minnesota, St. Paul, MN. 296 pages. (Cited in Negrón and Popp 2009).
- Hansen, E. M. 1996. Western balsam bark beetle, *Dryocoetes confusus* Swaine, flight periodicity in northern Utah. Great Basin Naturalist 56:348–359.
- Jeans-Williams, N. L., and J. H. Borden. 2006. Evaluation of Two Pheromone Baits for Containment and

- Concentration of Attack by the Western Balsam Bark Beetle, *Dryocoetes confusus* (Coleoptera: Curculionidae). Western Journal of Applied Forestry 21:27–32.
- Johansson, L., J. Andersen, and A. C. Nilssen. 1994. Flexible generation time in *Dryocoetes autographus* (Ratz.) (Col., Scolytidae): a key to its success as colonist in subarctic regions? Journal of Applied Entomology 117:21–30.
- **Langor**, **D. W. 1987.** Emergence, host attack, and overwintering behaviour of the eastern larch beetle, *Dendroctonus simplex* Leconte (Coleoptera: Scolytidae), in Newfoundland. The Canadian Entomologist 119: 975-983.
- Lindgren, B. S. 1983. A multiple-funnel trap for scolytid bark beetles. The Canadian Entomologist 115:299–302.
- Maclauchlan, L. E., L. Harder, J. H. Borden, and J. E. Brooks. 2003. Impact of the western balsam bark beetle, Dryocoetes confusus Swaine (Coleoptera: Scolytidae), at the Sicamous Research site, and the potential for semiochemical based management in alternative silviculture systems. Journal of the Entomological Society of British Columbia 100:27–41.
- Mathers, W. G. 1931. The biology of Canadian bark beetles. The seasonal history of *Dryocoetes confusus* Sw. The Canadian Entomologist 68:247–248.
- Negrón, J. F., and J. B. Popp. 2009. The flight periodicity, attack patterns, and life history of *Dryocoetes confusus* Swaine (Coleoptera: Curculionidae: Scolytinae), the western balsam bark beetle, in north central Colorado. Western North American Naturalist 69(4):447–458.
- Number Cruncher Statistical System. 1988. Kaysville, Utah, USA.
- Schmid, J. M., and R. H. Frye. 1977. Spruce beetle in the Rockies. USDA Forest Service General Technical Report RM-49. Fort Collins, Colorado.
- Schmitz, R. F., M. D. McGregor, and G. D. Amman. 1980. Mountain pine beetle response to lodgepole stands of different characteristics, pp. 234–243. *In* A. A. Berryman and L. Safranyik (Eds.) Proceedings of the second IUFRO conference on dispersal of forest insects: Evaluation, theory, and management implications. Sandpoint, Idaho. 27-31 August 1979. Cooperative Extension Service, Washington State University, Pullman, WA.
- Stock, A. J., J. H. Borden, T. L. Pratt, H. D. Pierce, Jr., and B. D. Johnston. 1995. Enantiomeric composition and release rates of *exo*-brevicomin influence aggregation of the western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). The Canadian Entomologist 127:449–456.
- Stock, A. J., J. H. Borden, and T. L. Pratt. 1993. Containment and concentration of western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae), populations by application of *exo*-brevicomin. Canadian Journal Forest Research 24:483–492.
- Stock, A.J., J.H. Borden, T.L. Pratt, H.D. Pierce, Jr., and B.D. Johnston. 1990. *endo-Brevicomin:* an antiaggregation pheromone for the western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). The Canadian Entomologist 122:935–940.
- Stock, A. J. 1981. The western balsam bark beetle, *Dryocoetes confusus* Swaine: secondary attraction and biological notes. M.Sc. Thesis, Simon Fraser University, B.C.
- **Veblen, T. T., K. S. Hadley, and M. S. Reid. 1991.** Disturbance and stand development of a Colorado subalpine forest. Journal of Biogeography 18:707–716
- Waters, H. J., and A. J. Stock. 1995. Application of MSMA to control western balsam bark beetle in subalpine fir —B.C. Ministry of Environment special use permit 103-414-92* Research File 48090-2 June 12 1992. Final report to B.C. Ministry of Environment, Pesticide Control Branch, January 1995. 13 p.
- Wermelinger, B., and M. Seifert. 1999. Temperature-dependent reproduction of the spruce bark beetle *Ips typographus*, and analysis of the potential population growth. Ecological Entomology 24:103–110.